





Research Article

Experimental evidence of negative agricultural impacts and effectiveness of mitigation strategies of invasive green iguanas (*Iguana iguana*) in Puerto Rico

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Abstract

Losses in crop yield due to invasive insects, weeds, pathogens, and herbivores cost trillions of dollars per year globally. To prevent further spread of invasive agricultural pest species, continuous monitoring and prevention are crucial. Once introduced, however, assessing the impact of an invasive pest on agricultural production and testing management strategies are essential. The green iguana (*Iguana iguana*), a globally widespread invasive herbivore, is considered a possible agricultural pest although no quantitative data on its impact are available. In this study, we evaluated the impact of the invasive green iguana on cucumber (*Cucumis sativus*, var. Dasher II) and lettuce (*Lactuca sativa*, var. Black-seeded Simpson) yield by testing the efficacy of two management strategies – Neem-based pesticide and mesh fencing – compared to open field cultivation in Puerto Rico. Mesh fencing led to 20% more growth and doubled cucumber yield compared to open field cultivation, while spraying Neem led to an 18% increase in plant growth but no effect on cucumber yield. We found no difference in lettuce growth or yield among treatment and control plots. This study supports categorizing the green iguana as an invasive agricultural pest species and demonstrates the reptile's potential to reduce crop yield. It also shows that Neem application at the manufacturer's suggested concentration is not an effective mitigation technique for reducing crop loss due to green iguana herbivory. Government agencies in regions where the green iguana has the potential to be introduced should consider the species a threat to food production when developing monitoring programs and drafting regulations.

Key words: Agricultural loss, biological invasion, cost of invasive species, exclusion experiment, invasive species in agriculture



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Introduction

Invasive species are a threat to global agricultural production (Paini et al. 2016); researchers estimate that invasive weeds, insects, pathogens, and other organisms lead to annual losses of \$1.4 trillion USD (Pimentel et al. 2001, 2005; Zenni et al. 2021). The potential impact of invasive species on agricultural production is highest for developing nations (Paini et al. 2016) that may lack the economic means to mitigate or manage invaders. Within these countries, small farmers are at the

highest risk due to their heavy reliance on their own food production as their main means for survival (Pratt et al. 2017). To support farmers and crop production, pest management plans are developed by policy makers to mitigate the detrimental impacts of invasive species on crop production (Stoddard et al. 2010; Ditomaso et al. 2017). A farmer's willingness to adopt mitigation measures is often tied to the recognition that a particular pest species is responsible for significant economic losses (Bajwa et al. 2019). Even when economic losses are realized, research on the effectiveness of different mitigation methods is often lacking.

Determining the extent of crop loss caused by a potential pest is critical for justifying prevention measures (Senar et al. 2016; Bajwa et al. 2019; García-Díaz et al. 2021). Exclusion studies are a useful tool in determining the severity of a pest species' impact on crop yield, as well as for testing management methods (Chouinard et al. 2017; Tollington et al. 2019). A study on cucurbits (e.g., cucumber, squash and melon) grown in high tunnels in Indiana (USA) sought to prevent pest beetles from accessing the plants (Ingwell and Kaplan 2019). Researchers tested three different mesh net sizes and found that intermediate nets were the optimal size for increasing yield. For some cucurbit varieties tested, yield was three times higher using the intermediate net size compared to no net, demonstrating the importance of testing management strategies to maximize crop yield. In addition to insect pests, exclusion netting has also been used to evaluate the impact of birds (Kuesel et al. 2019) and bats (Maas et al. 2019; Tollington et al. 2019) on crop yields. Though exclusion is widely used to protect crops, this strategy does not always increase crop yield (Maas et al. 2013). For example, a study on the coffee berry borer in Hawai'i assessed the impact of mesh netting on borer infestation levels, coffee quality, and coffee yield (Johnson et al. 2020). Researchers found higher borer densities in no-netting control plots but no differences in coffee quality or yield among treatments. Experiments to determine the effectiveness of management strategies are thus critical for providing useful management tools for the farming community.

Management recommendations aimed at reducing the negative impact of pest species often focus on controlling pest populations (García-Díaz et al. 2021) rather than mitigation strategies. In agriculture, population control (i.e., eradication or reduction in population size) for larger vertebrate species is difficult because pesticides cannot be used. Research on invasive vertebrates in the U.S. highlights the difficulties of implementing eradication and control measures (Witmer et al. 2007; Witmer and Fuller 2011). For example, eradication efforts targeting sheep in Hawai'i's Mauna Kea Forest Reserve have been unsuccessful despite the removal of 87,000 sheep by aerial hunting over a 75-year period (Hess and Jacobi 2011). Researchers and practitioners agree that developing management techniques beyond population reduction is necessary for future success (Witmer and Fuller 2011).

Testing invasive species management techniques on farms can have the two-fold benefit of providing policy makers with important information regarding the efficacy of management techniques while quantifying the economic impact needed to justify the development of pest management schemes. A good system to investigate this approach is the green iguana (*Iguana iguana*, Linnaeus, 1758), a widespread invasive species for which little information about its impact or management exists. The green iguana is native to Central and South America but has expanded its range most notably during the 1990's through the pet trade (Stephen et al. 2012). It can now be found on islands of the Pacific, the state of Florida, and the Greater Caribbean Region, among other places (Falcón et al. 2012; van den Burg et al. 2020; De

Jesús Villanueva et al. 2021). This reptile is a generalist herbivore and can exist in a wide variety of vegetative communities (Bughardt and Rand 1982). Information on the diet of this species is limited to a handful of studies in its native and introduced ranges. In Mexico, gut content identification found mostly *Ipomoea* sp. (the sweet potato genus) and *Tabebuia* sp. (a woody tree genus) as part of its native diet (Lara-López and González-Romero 2002). In Puerto Rico, mangroves (*Rhizophora mangle*, *Avicennia germinans*), pond apple (*Annona glabra*), and the yellow flamboyant tree (*Pelophorum pterocarpum*) were identified through isotopic analysis and germination of seeds found in feces (Govender et al. 2012; Burgos-Rodríguez et al. 2016). In Fiji, anecdotal accounts of green iguana foraging in village food gardens have reported *Ipomoea* sp. and Dalo (an important root crop, *Colocasia* sp.) as diet items, although the authors believe that more evidence is needed to consider the species a threat to food production (Kern 2009; Van Veen 2011; Shah et al. 2020). Based on interviews with the farming communities in Puerto Rico, researchers identified more than 30 crop species consumed by green iguanas, with squash (Cucurbitaceae) and tomato (Solanaceae) crops being among the most consumed (De Jesús Villanueva et al. 2022).

The green iguana's impact on agriculture is often cited by researchers and wildlife professionals as negative (López-Ortiz et al. 2012; López-Torres et al. 2012), although research on the topic is only just emerging (Rodríguez Gómez et al. 2020; De Jesús Villanueva et al. 2022). In Puerto Rico, where the green iguana has been documented since 1964 (Rivero 1998; De Jesús Villanueva et al. 2021), the species is popularly considered an agricultural plague (ElNuevoDia.com 2009; López-Ortiz et al. 2012). Work by De Jesús Villanueva et al. (2022) found that farmers on the island manage this species to prevent crop loss. Hunting, physical barriers (e.g., nets or metal fencing), changes in crop choice, and chemical deterrents were among the management practices reported. The local Department of Natural Resources and the Environment has recommended the use of Neem oil (*Azadirachta indica*) as a repellent, together with the removal of eggs from nests (López-Ortiz et al. 2012; López-Ortiz 2013). None of these management practices or recommendations have been evaluated for effectiveness, leaving their utility up to the perceptions of the practitioners.

In this study, we sought to quantify the impact of the green iguana on agricultural production and to test the utility of currently employed management techniques. To determine if green iguana management on farms leads to increased crop yield, we used two agricultural crops reported as impacted by the green iguana in Puerto Rico, cucumbers (*Cucumis sativus*) and lettuce (*Lactuca sativa*), and two management techniques, mesh fences and Neem-based repellent (De Jesús Villanueva et al. 2022). We tested these management techniques at two agricultural experimental stations in Puerto Rico, where based on the findings of De Jesús Villanueva et al. (2022), we expected green iguana herbivory to significantly reduce crop yields. We compared crop yields in our experiment to observed yields prior to the presence of green iguanas on farms in Puerto Rico (Abrams et al. 1976).

Methods

Site description

We conducted experiments at two agricultural experimental stations (AES) on the Caribbean island of Puerto Rico. These AES are part of the University of Puerto Rico Mayagüez agricultural extension program and are in the towns of Juana Díaz

(18.032318, -66.528910) and Gurabo (18.255926, -65.987933). We chose these two sites to conduct our experiments based on observations by field station agronomists of green iguana-related crop loss at each site and our own confirmation of the presence of green iguanas at each AES. To confirm the presence of green iguana on the two sites, we used visual encounter surveys (VES) at both field sites. The VES were repeated once a week for two months from June to August 2019. During the VES, three observers on average walked along each farm's fence line in a linear path adjacent to the experimental site for 200 m. Observations began at 0800 h and continued at a steady pace, stopping only to take note of the observations, until the 200 m length had been walked. Observations were made by eye, and binoculars were used to confirm observations when necessary. The climatic and soil conditions of the two sites were distinct from one another (see Suppl. materials for further details). The Juana Diaz Experimental Station is at an elevation of 0.0 Meters Above Mean Sea Level (MAMSL), and it is within the semi-arid climatic zone of the island (Goyal and Gonzalez 1989). The Gurabo Experimental Station is at an elevation of 52.0 MAMSL, and it is located within the moist climatic zone (Goyal and Gonzalez 1989).

Plant cultivation

To test how green iguanas may affect the cultivation and harvest of crops, we focused on two crops commonly grown in Puerto Rico: lettuce, *Lactuca sativa* (var. Black-seeded Simpson) and cucumber, *Cucumis sativus* (var. Dasher II). Lettuce and cucumber seedlings were purchased from local germination companies and transplanted into mulched plots covered in black plastic (4.6 m long by 1.5 m wide) at each AES. In each plot, 15 plants of either lettuce or cucumber were planted. Spacing between plants within the plots was 0.3 m and staggered in a zig-zag pattern (Fig. 1). Conventional fertilization regimes were used for each crop following the published agricultural extension guidelines and the recommendations of field station agronomists (Hernandez and Beaver 2015). A total of 1.81 kg of 10-10-10 +3Mg 1% trace elements were applied to all plots prior to planting. We used drip irrigation with 30.5 cm of hose between each emitter, which was positioned beneath the plastic mulch. Irrigation was done to saturation once or twice daily for up to 1 hour.

Treatment design

Each plot was randomly assigned to one of three treatments, Neem oil (chemical deterrent), mesh fence (physical barrier) or control (open field cultivation with no Neem or fence) using the package agricolae v 1.3-3 (De Mendiburu 2014) in R (R Core Team 2021). To assess the design and sample size needed to evaluate the impact of the green iguana on crop yield under these three treatments at two field sites, we performed a power analysis for a linear mixed model (Green and MacLeod 2016) in R. We first simulated pilot data for the Juana Diaz and Gurabo field sites. In each site, we simulated 10 plots for each treatment, each with 15 plants (i.e., totaling 900 simulated lettuce plants). We then simulated that the highest probability of survival and growth would occur in our fenced treatments, with 1% death in the fenced treatment, 6% death for the neem treatment, and 8% death for the control treatment. If plants survived, we simulated the number of leaves for each plant and recorded the power to detect a significant fixed effect for different effect sizes using the R package simr v 1.0.7. From this analysis, we observed high power (>80%) to

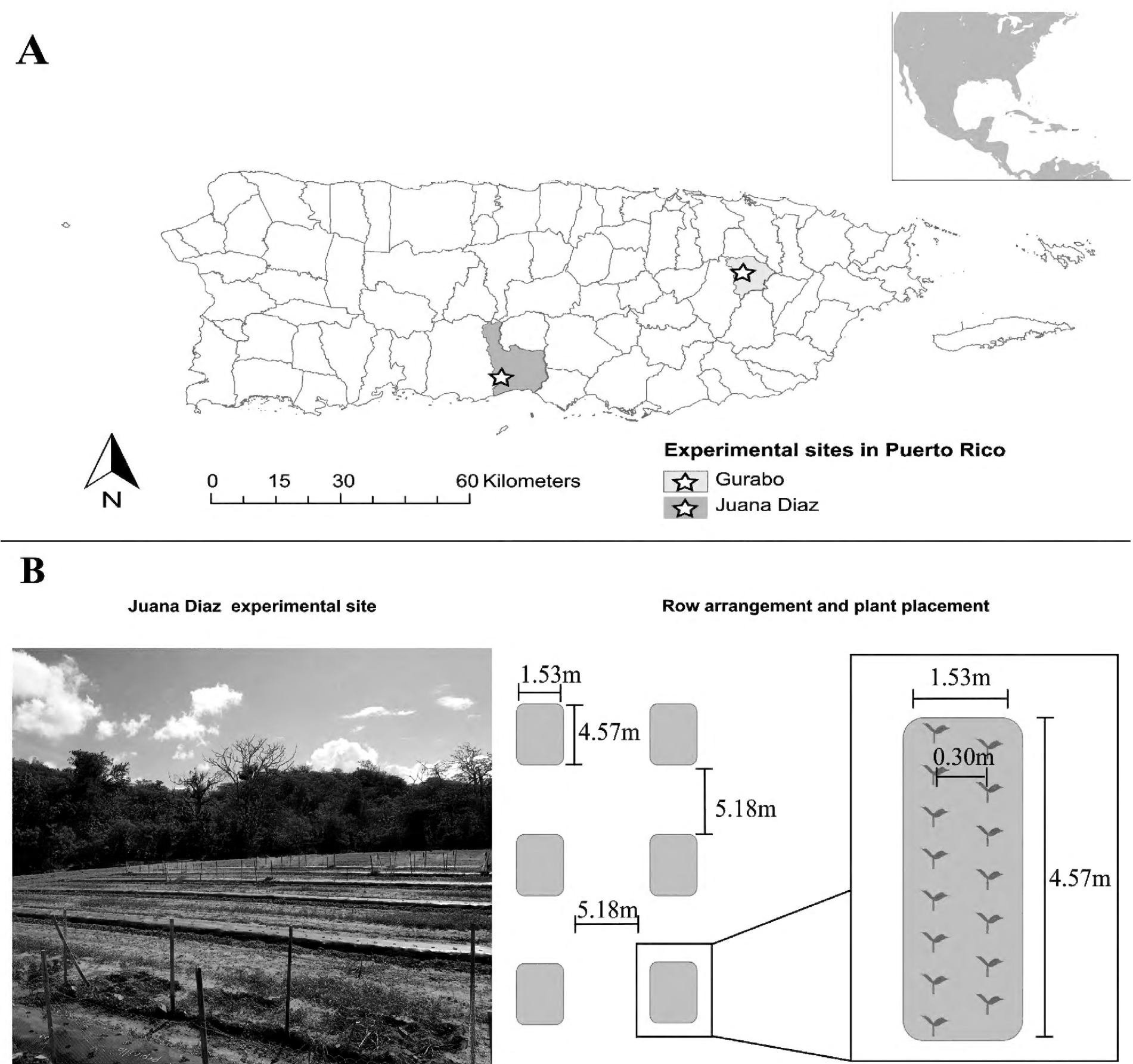


Figure 1. **A** location of experimental sites in Puerto Rico and **B** view of study plots at the Juana Diaz Agricultural Experimental Station with a schematic showing the dimensions and spacing of plots and plants used in the study.

detect a significant difference for sample sizes of more than 10 plants per plot for a moderate effect size of 0.3 or larger between control and neem versus the fence treatment. R script for our power analysis is provided in the Suppl. material 2.

Based on the results of our power analysis, at both the Juana Diaz and Gurabo Experimental Stations, each treatment was replicated 10 times for a total of 30 plots of each crop, that is, 60 plots total for the two crops (i.e., 10 plots each of lettuce and cucumber in each of control, fence, and Neem treatments, Fig. 2). This resulted in a total of 450 plants of both lettuce and cucumber at each AES. All treatments had the same irrigation and fertilization regimes and, if necessary, pesticide applications. Cucumber plants were sprayed once with DiPel DF (a biological insecticide based on *Bacillus thuringiensis*) in Juana Diaz to treat a common foliar infection by *Diaphnia* spp. Plots were separated by 5.2 meters and placed parallel to the forested edge of the farm at each AES.

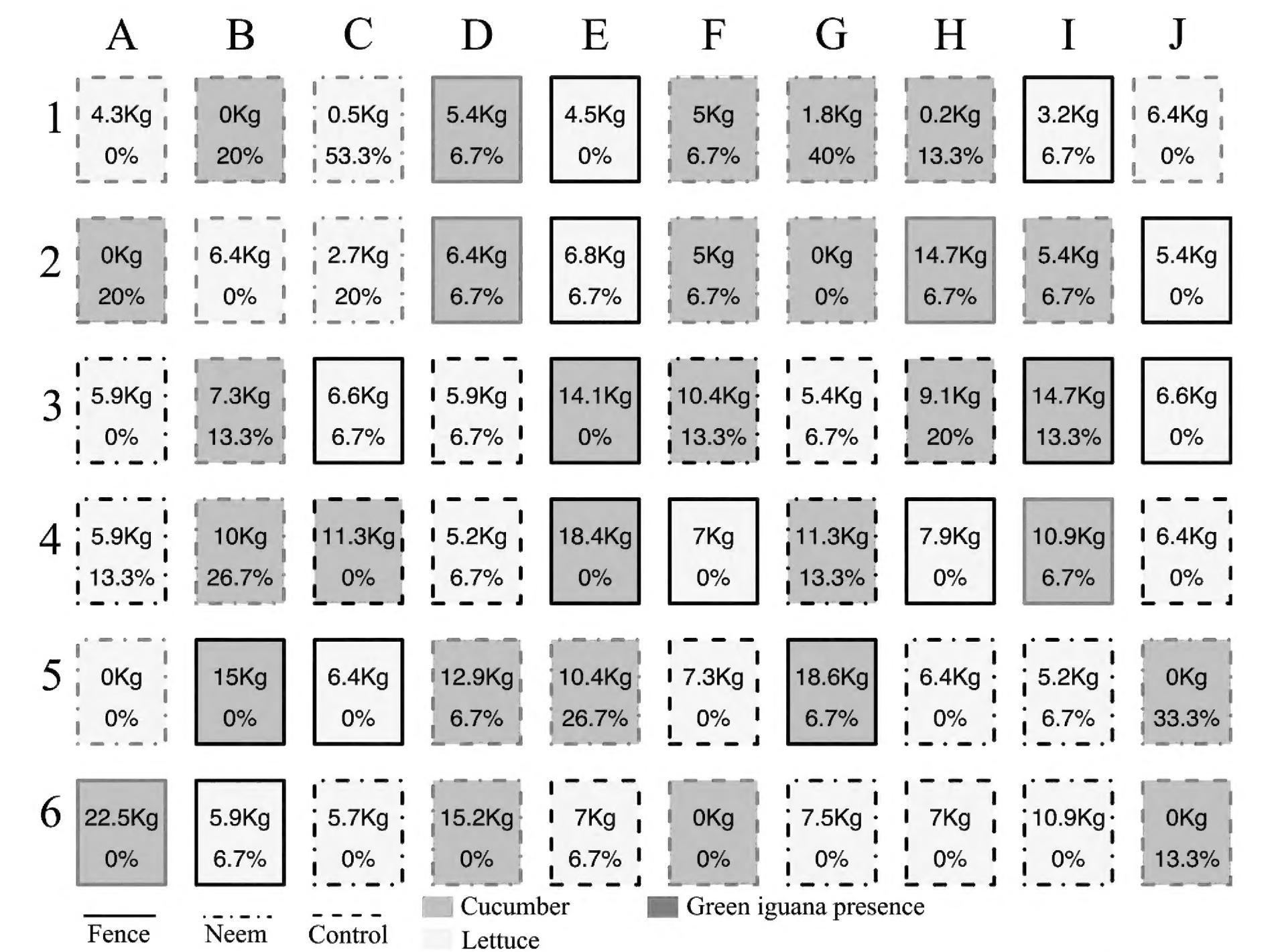


Figure 2. Spatial arrangement of plots at the Juana Diaz Agricultural Experimental Station experimental site. Yield (Kg) and mortality (%) are shown for each plot. The border line pattern indicates the experimental treatment, red lines indicate the presence of green iguanas in the plot, and the rectangle fill color indicates the species of crop planted. Row 1 was the closest to the forest edge.

All treatments were subjected to the irrigation, fertilization, and pesticide application as described above and no further actions were taken for control plots. For the two experimental treatments, additional steps to deter green iguana herbivory were taken. In our first experimental treatment, we used a commercially available chemical deterrent called Trilogy™ (Certis USA), which is an organic foliar pesticide derived from Neem plants (*Azadirachta indica*). It was sprayed directly onto plants once per week by the station staff using a backpack sprayer for the duration of the experiment following the manufacturer’s suggested dilution of 1%. For our second experimental treatment, we physically fenced in crops with a nylon monofilament fishing net (Lee Fisher Company, www.leefisherfishing.com). Net openings when fully tensed were 7.0 cm in size, the height of the net when tensed was 1.7 m, though in our treatment 0.6 m of the net was buried to prevent green iguanas from digging underneath the fence. To reduce the ability of green iguanas to climb on the surface, the nets were not fully taut and left hanging slightly off their posts (Fig. 1).

Data collection

For the duration of the experiment, we monitored green iguana presence and documented instances of herbivory through researcher observations and six camera traps (Foxelli Mod No. 57047, interspersed among plant treatments at edges and

center of the experiment) at each experimental site. For cucumbers, we attributed plant herbivory to green iguanas when entire leaves were removed and only the petiole remained. If we observed leaves with other forms of damage (Suppl. material 1: fig. S1), this was not attributed to the green iguana. We measured the distance from the center of each plot to the forest adjacent to our experimental site as a measure of the minimum distance green iguanas would need to travel to reach the crops. To monitor plant growth during the experiment, we individually marked plants and counted the number of leaves on each plant daily during the first week of the experiment, then every other day for the remaining 31 days. If the number of leaves decreased over time, we considered this a sign of green iguana herbivory. Once the number of leaves surpassed 20 on a cucumber plant and the plants became entangled, and over 25 leaves on a lettuce plant, we monitored survival until harvest. After 42 days, we (4 persons) harvested the lettuce plants and cucumbers produced in each treatment. We documented the number of heads of lettuce produced in plots and their total weight, as well as the number of cucumbers and their total weight. Cucumbers had an additional second harvest based on the maturity of the fruit that occurred 10 days after the first harvest at Juana Diaz Experimental Station and two days after the first harvest at Gurabo Experimental Station.

Statistical analyses

We calculated the mean and standard deviation of plant growth and harvest yield for cucumber and lettuce plants using R in R studio (R Core Team 2021; RStudio Team 2021). We fit a Cox proportional hazards model using the *coxph* function in the R package *survival* (v3.2-7; Therneau, 2020) to test the effect of our treatments on plant survival over time. We fit a generalized linear mixed model (GLMM) by REML using the *lmer* function in the R package *lme4* (Bates et al. 2015). We included the variables treatment (i.e., control, Neem, and fence) and distance to the edge of the forest as fixed effects in our model and plant ID and plot within the field site as random effects. To evaluate the relationship between these variables and our response variables of plant growth and yield, we used the number of leaves as a measure of growth and either plant or fruit weight as a measure of yield. In the plant growth GLMM we included both plant ID and plot location as random effects, while for yield we only included plot location as a random effect. The latter variable, yield, was square-root transformed to improve normality based on our evaluation of its distribution using the function *descdist* from the R package *fitdistrplus* (Delignette-Muller and Dutang 2015). To compute confidence in the GLMM, we used the R package *parameters*, which allows the user to report standard error and p-values among the results of their statistical models (Lüdtke et al. 2020). We used the function *parameter*, which provides coefficients, standard errors, confidence intervals, t-values, and p-values at the intercept for fixed effects.

Results

During our pre-planting visual encounter survey (VES), we observed higher green iguana presence in Juana Diaz (289 lizards in 6 days, Fig. 1) compared to Gurabo (11 lizards in 5 days). The presence of green iguanas at the Juana Diaz Experimental Station was first noted on 8 September 2019, five days post-planting. This was confirmed by iguana tracks, camera trap images, and herbivory damage (Fig. 3).

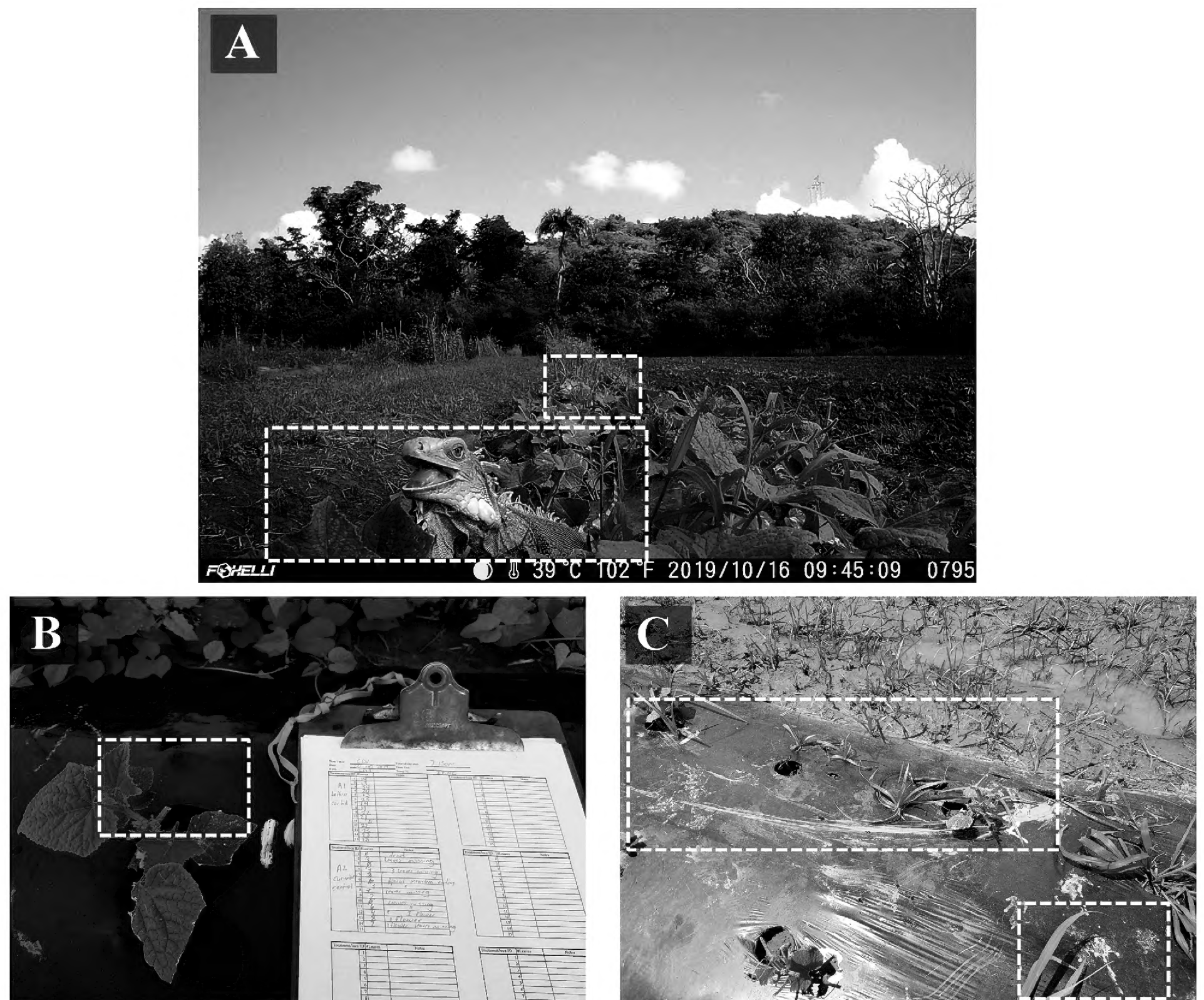


Figure 3. Evidence of green iguana presence at the Juana Diaz Agricultural Experimental Station study site. Six camera traps were used to monitor for green iguana activity **A** photo showing two green iguanas in a cucumber control plot **B** photo documenting evidence of green iguana herbivory on a cucumber plant in a control plot. We considered plants with only a leaf petiole (and no leaf) as evidence of green iguana herbivory as opposed to instances of leaf damage indicative of insect herbivory **C** photo showing claw and tail marks on the plastic mulch liner used to control weed growth.

By harvest, 22 out of 60 plots in Juana Diaz showed green iguana activity (Fig. 2). No green iguana evidence was found in Gurabo study plots during the experiment, though they were observed on the property before and after the study. Gurabo's mean yield data serves as an example of yields without iguana herbivory, showing no significant differences among treatments for lettuce or cucumbers (Suppl. material 1: fig. S2). We therefore focus the rest of our results on the Juana Diaz Experimental Station.

Photos from camera traps confirmed green iguana herbivory at Juana Diaz, with no other large herbivores observed (Suppl. material 1: fig. S3). One camera trap video captured a green iguana eating a lettuce leaf fragment in a control plot (Plot J1, Fig. 2), and the plant survived until harvest. In cucumber plots, iguana herbivory occurred in 17 of 30 plots, including 8 control, 7 Neem-treated, and 4 fenced plots.

Because we only documented or observed one incidence of herbivory on lettuce, and because there was no difference in growth or yield of lettuce as a function of our treatments (Fig. 2), we focus our results on cucumber plant growth and yield. At the

Juana Diaz Experimental Station, cucumber plant growth based on the number of leaves was on average 18% higher in the fence treatment compared to the Neem treatment and 20% higher compared to the control plots (Table 1, Fig. 4). Cucumber plant mortality was 49 out of 450 plants or 11% (Fig. 2), with the lowest mortality occurring in fenced treatment plots (7 plants or 2%), followed by control plots (17 plants or 4%) and highest in the Neem treatment plots (25 plants or 6%). Results from the survival analysis (Fig. 4) showed that individuals in the fenced treatment had the lowest likelihood of mortality across most of the experiment ($P = 0.046$).

Our square-root transformed cucumber growth and yield data provided a better GLMM fit based on skewness (growth = 0.78, yield = -0.29), lower AIC values (Suppl. material 1: table S1) and in the Cullen and Frey graph of skewness versus kurtosis, which demonstrated approximation to normality. The GLMM analysis for cucumber growth showed that plants in the fenced treatments had higher growth than in the control plots ($P < 0.001$), but that plant growth in the Neem treatment did not differ from the control ($P = 0.75$). The GLMM analysis also showed that yield was higher for plants in the fenced plots ($P < 0.001$) compared to the control plots, but only nearly so in the Neem treatment compared to control ($P = 0.071$), and that plots farther from the forest edge had higher growth ($P < 0.001$) and yield ($P = 0.052$) (Table 2). Mean cucumber yield in the fenced treatment was 15.50 kg (34.17 lbs.; 551 cucumbers), which was over three times the yield of control plots (5.09 kg or 11.22 lbs.; 196 cucumbers) and twice the yield of Neem plots (7.63 kg or 16.82 lbs.; 337 cucumbers) (Table 3).

Table 1. Observations of green iguana occurrence made during visual encounter surveys (VES) along a 200-m transect adjacent to the fence line next to planting sites within the two Agricultural Experimental Station farms in Puerto Rico. Blanks are left for days where VES were completed in one site but not the other.

Farm	2019 Visual Encounter Survey dates										Total
	June 26	July 09	July 16	July 18	July 23	Aug 01	Aug 02	Aug 06	Aug 08	Aug 16	
Juana Diaz		43	51		46	55		52		42	289
Gurabo	0			6			0		2	3	11
										Total	300

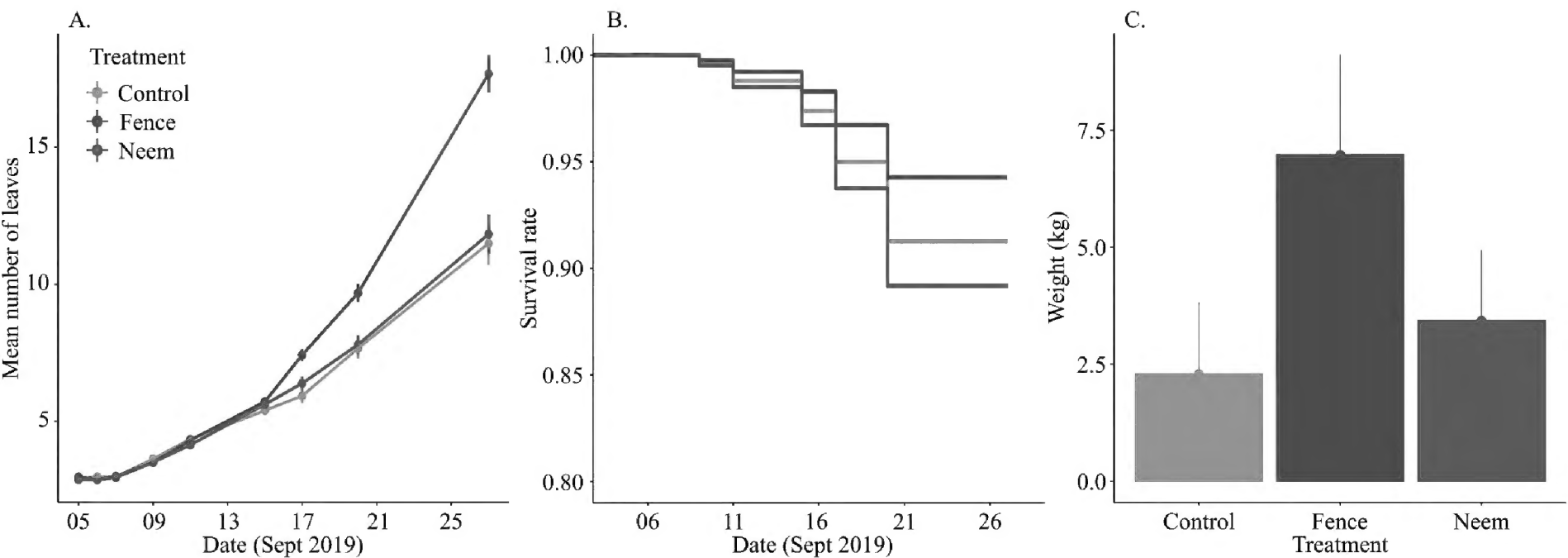


Figure 4. At the Juana Diaz Agricultural Station **A** mean (\pm SD) for the number of leaves as a measure of cucumber growth by treatment. An increase in leaf number indicates plant growth **B** survival analysis comparing cucumber survival among treatments. Cucumbers in the fence treatment had a higher likelihood of survival over the course of the experiment ($P = 0.046$) **C** mean (\pm SD) for cucumber yield by treatment.

Table 2. Parameter estimates of fixed effects from generalized linear mixed model (GLMM) of cucumber growth and yield. We used the *lmer* function and fit the model by REML in the R package *lme4* (Bates et al. 2015).

	Effect Estimate	SE	t value	Confidence interval lower 95	Confidence interval upper 95	p
Growth						
Intercept (Control)	1.82	0.08	21.76	[1.66]	[1.99]	<0.001
Cucumber Fence	0.20	0.05	3.82	[0.10]	[0.30]	<0.001
Cucumber Neem	0.02	0.05	0.32	[-0.08]	[0.12]	0.75
Distance to forest	0.0061	0.0015	3.99	[0.00]	[0.01]	<0.001
Yield						
Intercept	0.004	0.89	0.004	[-1.74	1.75]	0.997
Cucumber Fence	2.06	0.45	4.59	[1.18	2.94]	<0.001
Cucumber Neem	0.81	0.45	1.80	[-0.07	1.69]	0.071
Distance to forest	0.03	0.02	1.95	[0.00	0.06]	0.052

Table 3. Mean (\pm SD), median (minimum, maximum) and total of cucumber yield (i.e., weight and number of cucumbers) for each treatment at the Juana Diaz Agricultural Experimental Station.

	Treatment			
Juana Diaz	Control (N = 20)	Fence (N = 20)	Neem (N = 20)	Total (N = 60)
Cucumber weight (Kg)				
Mean (SD)	5.09 (± 7.28)	15.50 (± 10.20)	7.63 (± 7.14)	9.41 (± 9.31)
Median [Min, Max]	0.670 [0, 21.5]	12.0 [3.00, 35.00]	8.00 [0, 24.50]	8.00 [0, 35.00]
Total yield	102	310	153	564
Number of cucumbers				
Mean (SD)	9.80 (± 14.10)	27.60 (± 15.00)	16.90 (± 12.90)	18.10 (± 15.60)
Median [Min, Max]	1.50 [0, 49.00]	25.00 [7.00, 52.00]	14.50 [0, 48.00]	15.00 [0, 52.0]
Total yield	196	551	337	1080

Discussion

Global agricultural production and food security is under immense pressure due to species invasions (Paini et al. 2016). In this study, we examined the impact that green iguanas have on cucumber and lettuce crop yield in Puerto Rico and tested techniques to mitigate the impact of this invasive reptile. Here we provide evidence of reduced crop yield and argue that the green iguana has the potential to significantly reduce agricultural yield in other important food crops in the tropics.

At a small research site (0.25 acres), we confirmed the detrimental effects of green iguanas on crop production previously reported in interviews with farmers (De Jesús Villanueva et al. 2022). Small scale farm data is considered a valuable source of information for understanding the effect of growing conditions on crop yield at larger scales (Huffman et al. 2015; Fry et al. 2017). The impact of the green iguana may have been conservative due to the regular presence of researchers, though it still led to significant differences in yield. In our study, the use of mesh fencing to exclude green iguanas increased cucumber yield by 50% when compared to using Neem and 67% compared to control plots. Abrams et al. (1976) estimated the yield of cucumbers (Gemini Variety) was 10 tons (9071.85 Kg) per acre at the Juana Diaz Experimental Station (then called Fortuna) before green

iguanas were present. In our experiment, we used ¼ of an acre, half of which was used for cucumber and further divided into the three treatments. Based on the area used in our experiment and Abrams et al.’s (1976) estimate, we expected a cucumber yield of 377.99 Kg. Our fenced treatment plots produced a yield of 310 Kg of cucumber, which is similar to those estimated by Abrams et al. (1976) 45 years ago without green iguana herbivory, whereas our yields for Neem (153 Kg) and control (102 Kg) plots were substantially less than the expected yield. Moreover, in the absence of green iguana herbivory, our Gurabo Experimental Station site showed no difference in cucumber yield among treatments (Fence = 179.60 Kg, Neem = 176.02 Kg, Control = 210.05 Kg, Suppl. material 1: fig. S2). This suggests that when green iguana herbivory does occur it has the potential to be a significant source of crop loss and ultimately economic loss.

The reductions in yield we observed in our Neem and control plots translate into potentially heavy economic losses for farmers who may be facing crop loss due to the green iguana and to the economy in general. By visiting five local food markets and distributors to determine the price of cucumbers, we were able to calculate the loss in revenue a Puerto Rican farmer would have faced on the island at the time of our harvest. In December 2019, a 25lb (11.33 Kg) box of cucumbers was being purchased wholesale at between \$19 and \$22 USD. Based on our harvest results, if a farmer would have used open field cultivation for cucumbers on one acre with plants experiencing green iguana herbivory, they would have sold their harvest at around \$4,429 USD (\$20.5 USD/ 11.33 Kg). In contrast, a farmer using mesh fencing to reduce green iguana herbivory would have sold their cucumbers for \$13,462 USD. Taking into account the cost of materials (estimated at \$134.00 for fencing) and labor (\$60 for 8 h in 2019), a net \$6,818 USD per harvest acre reduction in income could be used to argue in favor of implementing this management technique (Table 4). Estimated costs of implementing mesh fencing as a mitigation measure for a 1-acre plot are provided in the Suppl. materials. Though we provide the estimated costs of implementing this measure, farmers should consider netting that is set deeper into the ground and taller over the crops to fully exclude this lizard.

Our results suggest that Neem is ineffective at deterring green iguana herbivory and may lead to decreases in plant growth. We do not recommend the use of Neem as a mitigation technique for green iguana herbivory, as it does not lead to higher yields compared to those observed when no mitigation technique was used (i.e., control plots). The use of mesh fencing to protect crops from green iguana herbivory is effective at improving crop yield, although the effectiveness of this mitigation tactic may decrease over time. We observed green iguanas inside our fenced plots on multiple occasions. The reptiles were able to climb the

Table 4. Estimated crop (cucumber) revenue under different techniques to mitigate crop loss due to green iguana herbivory.

Management technique/ Cultivation strategy	Cucumber revenue (USD)/acre ¹
Control (open field)	4,429.30
Mesh fences	13,461.80
Neem (<i>Trilogy</i> ™ <i>Certis USA</i>)	6,643.95

¹Value per acre was estimated based on the yield produced at our Juana Díaz Agricultural Experimental Station, and the median value of cucumbers (20.5USD/ 11.33Kg) in Puerto Rico in December 2019.

fences, with some fenced treatments having more than one green iguana inside it at the same time (<https://youtu.be/D7rIb71XF8Y>). Weekly, or perhaps daily, maintenance of the fences is necessary throughout cultivation to ensure their integrity. To maintain fences in our experiment, we had to contend with weeds that would grow on our fence and pull it toward the ground, and heavy rains that washed soil away from the portion of mesh that was buried, resulting in the need to re-fit and seal gaps in the fences. At a farm, this would entail labor and material expenses that would need to be considered when scaling up to larger production. Durable fence material can be reused with careful planning to prevent knotting, which would reduce production costs. At larger scales, durability should be prioritized to ensure the investment in materials does not negate the revenue produced from seeking to increase yield. Methods to protect crops could be combined with other management techniques to further prevent crop loss such as done with other species (Rivadeneira et al. 2018). In birds, for example, exclusion netting is sometimes combined with lethal, auditory, and visual deterrents to prevent crop damage. Additional methods could be tested and used in combination with netting to attempt to increase crop protection.

Farmers should be provided with technical and financial assistance to implement green iguana mitigation strategies. This support might be particularly urgent for smaller farms that may suffer greater relative impacts. As documented here, the crop's plants grown in plots on the edge of our site closer to the forest (Fig. 2) were more susceptible to herbivory from green iguanas than those in the center of the field. Choosing to plant crops that are not part of the green iguana diet in edge plots may help decrease crop loss (De Jesús Villanueva et al. 2022), but this technique needs to be evaluated experimentally. In addition to recommendations on crop choice and cultivation location, considerations based on green iguana phenology should be made. As seen with other pest species (Murray 2008; Crimmins et al. 2020), phenology, or the relationship between a species yearly life cycle and the environment, can significantly impact the effectiveness of mitigation measures. Considering green iguana phenology (i.e., diet, reproductive cycle, relationship to daily and yearly environmental temperatures) when designing management recommendations may be critical to successful implementation. For example, farmers could be advised to avoid accumulating soil or plowing when green iguanas are in their nesting season to prevent the creation of nesting sites on the farm. Future work should focus on exploring the relationship between green iguana phenology and crop loss to ensure relevant management recommendations are made.

Our study focused on testing farm-level mitigation measures to decrease green iguana related crop loss. It is widely recommended, however, that preventing invasive species introduction altogether is a much more cost effective strategy than post-introduction management (Lodge et al. 2006). As a crop protection measure, we urge governments to strengthen their biosafety protocols to prevent green iguanas from becoming introduced. In regions where the risk of introduction has been identified (see Falcón et al. 2012, 2013), green iguanas should be included in invasive species monitoring programs. If programs have not been established, public species inventory programs (e.g., www.iNaturalist.org) can be used as a means of early detection (van den Burg et al. 2020). In places where a species has already been introduced, the potential for economic loss through herbivory should be addressed. If there is a lack of empirical evidence to support considering the green iguana as an agricultural pest, anecdotal accounts of the species damaging food

crops should be considered as an early warning sign (Shah et al. 2020). Governmental and non-governmental agricultural management offices should keep close documentation of these anecdotal accounts to gain an understanding of the extent to which green iguanas could present a problem.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: JJK, CNDJV. Data curation: GPMP, CNDJV. Formal analysis: SVB, CNDJV, JJK. Funding acquisition: JJK, CNDJV. Investigation: GPMP, CNDJV, JJK. Methodology: CNDJV, SVB, JJK. Project administration: JJK, CNDJV. Resources: JJK, WG. Supervision: JJK. Visualization: SVB, CNDJV. Writing - original draft: JJK, CNDJV. Writing - review and editing: GPMP, WG, JJK, SVB, CNDJV.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Supplementary information

Authors: Christina N. De Jesús Villanueva, Gabriela P. Massanet Prado, Steven M. Van Belleghem, William Gould, Jason J. Kolbe

Data type: docx

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Supplementary material 2

A revision power analysis script R

Authors: Christina N. De Jesús Villanueva, Gabriela P. Massanet Prado, Steven M. Van Belleghem, William Gould, Jason J. Kolbe

Data type: R file

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Supplementary material 3

Revision statistical analysis script R

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Data type: R file

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Supplementary material 4

Revision study data

Authors: Christina N. De Jesús Villanueva, Gabriela P. Massanet Prado, Steven M. Van Belleghem, William Gould, Jason J. Kolbe

Data type: csv

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